

Species limits in the pygmy antwren (*Myrmotherula brachyura*) complex (Aves: Passeriformes: Thamnophilidae): 1. The taxonomic status of *Myrmotherula brachyura ignota*

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Abstract.—The taxonomic position of a trans-Andean avian population described as *Myrmotherula brachyura ignota* Griscom, 1929, has existed under a cloud of uncertainty for the past fifty years. Recent advances in the use of vocalizations in species-level taxonomy in suboscines, generally, and thamnophilids, specifically, provide a basis for a reexamination of the relationships of *M. b. ignota* to two closely related cis-Andean taxa, *M. brachyura* and *M. obscura*. Four independent vocal characters distinguish *M. b. ignota* from *M. brachyura*, whereas the vocalizations of *M. b. ignota* cannot be distinguished from those of *M. obscura*. *Myrmotherula b. ignota* and *M. obscura* also share plumage characters distinct from *M. brachyura*. *Myrmotherula ignota* is recognized as a distinct species, Moustached Antwren, of which *M. i. obscura* is a subspecies.

Smallest of the typical antbirds (Thamnophilidae), *Myrmotherula brachyura* was also one of the first in its family to be described (Hermann 1783). Unlike most thamnophilid species with widespread distributions for which a plethora of subspecies were described in the following almost 150 years, *M. brachyura* remained a monotypic species as late as 1924 (Cory and Hellmayr 1924) with a geographic range extending throughout Amazonia, the Guianas, and the region immediately northwest of the Andes. In 1929, the trans-Andean population in Panama and Colombia (now known to extend to northwestern Ecuador) was described as *M. b. ignota* (Griscom 1929) based on the briefest of descriptions: “Similar to typical *M. brachyura* of Cayenne and Amazonia, but the light streaking on pileum, wings, and back greatly reduced, resulting in more solidly blackish areas; female with much paler rufous crown stripes, and no fulvous on throat.”

Zimmer (1932), after examining about 100 cis-Andean specimens of *M. brachyura*,

noticed that some were “sharply distinguishable.” He stated that if these specimens were found in allopatry with *M. brachyura*, he would have considered them conspecific, but because they occurred at the same locations as *M. brachyura*, he described them as a new species, *Myrmotherula obscura*, Short-billed Antwren. Zimmer’s diagnosis and descriptions were much more complete than those of Griscom, but the salient points can be summarized as follows. Compared to *M. brachyura*, male upperparts and wings much darker (black), black mystacial stripe and black postocular stripe much broader, and length of bill reduced (ranges of measurements of exposed culmen abut but do not overlap); female with pale head markings narrower and more rufescent, back markings narrower and whiter, and mystacial streak, postocular area, and bill length differed like male. The geographic range of *M. obscura* has since been found to extend through southeastern Colombia, eastern Ecuador, northeastern Peru,

and extreme west-central and southwest Amazonian Brazil.

In his description Zimmer (1932) did not compare specimens of *M. obscura* and *M. b. ignota*, apparently because he only had one male specimen of *M. b. ignota* at hand. *Myrmotherula b. ignota* is an uncommon bird in the field and in collections, and the paucity of specimens has hampered understanding of its taxonomic position. However, the similarity of plumage characters distinguishing *M. b. ignota* and *M. obscura* from *M. brachyura* is apparent from the descriptions. Subsequently, the similarity caused Bond (1950), who had obtained two additional female-plumaged specimens of *M. b. ignota*, to consult Hellmayr on the possibility that they could be more closely related to *M. obscura* than to *M. brachyura*. Their conclusions were inconclusive, confused by the finding that bill lengths of *M. b. ignota* fell into the range of those of *M. brachyura*, and Zimmer had emphasized bill length as an important character separating *M. brachyura* and *M. obscura*. Their considerations, however, led Meyer de Schauensee (1966) to write "It is possible that what is currently called *M. brachyura ignota* from Panama and northwest Colombia may prove to be specifically distinct from *M. brachyura* and conspecific with *M. obscura* . . ." Most recently, the seventh edition of the Check-list of North American Birds (American Ornithologists' Union 1998) noted the possibilities that *M. b. ignota* might be specifically distinct or more closely related to *M. obscura* than to *M. brachyura*.

Today, bolstered by the growing understanding that vocalizations in nearly all suboscines (including the Thamnophilidae) are innate, vocal characters are increasingly employed in examining species level questions in these families (Baptista & Kroodsma 2001). In an effort to provide a point of reference for considering species limits in the Thamnophilidae using vocal characters, Isler et al. (1998) compared characteristics of vocalizations of eight pairs of closely re-

lated but reproductively isolated, syntopic antbird species. Among these were *M. obscura* and *M. brachyura*, whose vocalizations in the region of sympatry were analyzed. Three independent vocal characters were found to distinguish loudsongs (sensu Willis 1967) of the two species, and in addition, each species included a call in its repertoire not known to be delivered by the other.

Given the diagnostic differences found between vocalizations of *M. obscura* and *M. brachyura*, an obvious question for empirical analysis is which of these species are the vocalizations of *M. b. ignota* most closely related? Earlier consideration of the question was hampered by the lack of vocal recordings of *M. b. ignota*, a situation similar to that facing earlier specimen comparisons. Ten years ago only one recording of *M. b. ignota*, a loudsong, was available. Its initial examination suggested that *M. b. ignota* was more closely related to *M. obscura* (M. & P. Isler, R. Ridgely in Ridgely & Tudor 1994), but the single example precluded analysis. Since then, a number of recordings of *M. b. ignota* have been obtained, and they allow us to address this fundamental question.

Methods

Because current species designations confuse rather than clarify the discussion, henceforth in this paper we refer to the three taxa simply as *brachyura*, *obscura*, and *ignota*.

Morphology.—Examination of specimens available at the National Museum of Natural History (USNM) indicated that descriptions of earlier authors (cited in the introduction) accurately reflected plumage coloration of the three taxa. Consequently, no additional plumage data were obtained. Because of the importance of bill measurements in the description of *obscura*, and because the differences in bill length between *ignota* and *obscura* deterred earlier workers from establishing a close relationship be-

tween the taxa, measurements of bill length were obtained, using MAX-CAL electronic digital calipers, from specimens of the Louisiana State University Museum of Natural Science, Baton Rouge, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru, and USNM.

Vocalizations.—The sample of recordings of *brachyura* and *obscura* used and referenced in an earlier study of vocal differences (Isler et al. 1998) was employed in this analysis. The sample was obtained in the vicinity of the lower Río Napo in northern Peru. The reason for confining the sample to this area was to obviate the possibility of introducing geographic variation in the vocalizations of the wide-ranging *brachyura* into the comparison. Analysis of geographic variation in the vocalizations of *brachyura* was beyond the scope of this paper but will be addressed subsequently.

Seven recordings of *ignota* from Panama and three from Ecuador were employed. The recordings were not yet archived in an institutional collection. They were obtained at the following locations (listed as country, department, locality) which are followed by the name of recordist and number of individuals recorded. PANAMA: Colón: Canal Zone (R. Ridgely 1, B. Whitney 3). San Blas: Nusagandi (B. Whitney 1). Darién: Cerro Pirre (B. Whitney 1), Cana (B. Whitney 1). ECUADOR: Esmeraldas: 30 km E San Lorenzo (D. Lane 1). Pichincha: 20 km N Pedro Vicente Maldonado (D. Lane, 2).

Recordings were analyzed using “Canary 2.1.4” software (Charif et al. 1995). Procedures for analyzing vocalizations of *brachyura* and *obscura* were described in the earlier paper (Isler et al. 1998). Vocalizations of *ignota* were analyzed as follows. First, sound spectrograms were printed of each recording to identify vocalization types and to permit visual comparisons among recordings. In each recording, the first three measurable loudsongs were selected for measurement. Measurements were directed to vocal characteristics that had been found to differ diagnostically in

the earlier comparisons of *brachyura* and *obscura*. Number of notes, duration, and pace (notes/sec) were obtained for the entire vocalization. Then, loudsongs were divided into five sections (Isler et al. 1998) to obtain the pace for each section and ratios of change of pace between sections. Measurements were also taken of the duration of the second, middle, and next-to-last notes and the spaces following them.

Finally, we determined whether vocal characters differed diagnostically between taxa, employing guidelines developed earlier (Isler et al. 1998, 1999). As described in more detail in the previous papers, such differences must be unambiguously distinct character states, or, in the case of continuous variables, ranges may not overlap and the means (\bar{x}) and standard deviations (SD) of the population with the smaller set of measurements (a) and the population with the larger set of measurements (b) must meet the requirement:

$$\bar{x}_a + t_a SD_a \leq \bar{x}_b - t_b SD_b \quad (1)$$

where t_i = the t -score at the 97.5 percentile of the t distribution for $n - 1$ degrees of freedom (except for ratios where this statistical test is inappropriate).

Results and Discussion

Morphology.—Principal plumage characters distinguishing the taxa are as follows. Males of *ignota* and *obscura* are similar to *brachyura* except mystacial streak is broader and more distinct, black postocular streak more prominent, and black of crown and upperparts more extensive. Male *obscura* differs from *ignota* in having fewer pale streaks and consequently more extensive black in the plumage, especially on upperparts. Female *ignota* and *obscura* similar to *brachyura* except malar and postocular streaks are more prominent (as in male) and light portions of head, throat, and breast are darker: tawny brown in *ignota*, and buff in *obscura* (distinguishing these two taxa) rather than white or white tinged buff as in *brachyura*.

Bill measurements were taken from a larger number of specimens of *ignota*, including the first specimens from Colombia, than were available to earlier authors. The mean of bill length (measured from the nares) for *ignota* in Panama is $8.4 \pm SD$ of 0.2 mm (range 8.2 to 8.8, $n = 8$); in Colombia the mean was $7.9 \pm SD$ of 0.2 mm (range 7.5 to 8.1, $n = 7$). Equivalent values for *obscura* in Peru are $7.5 \pm SD$ of 0.3 mm (range 6.8 to 8.1, $n = 16$), and those for *brachyura* (various countries) are $8.7 \pm SD$ of 0.3 mm (range 8.4 to 9.3, $n = 8$). These values confirm the difference in bill length between *ignota* in Panama and *obscura* found by earlier authors, but they also show that bill length of *ignota* in Colombia is intermediate, suggesting the possibility of clinal variation between populations of *ignota* in Panama and *obscura* in Amazonia.

Vocalizations.—The earlier study of vocal differences between *brachyura* and *obscura* (Isler et al. 1998) concluded that there are at least four independent vocal characters that distinguish the two taxa. These vocal differences, although primarily determined by measurements, are also evident in visual comparisons of sound spectrograms (Fig. 1). The examples shown in the figure are typical for each taxon, i.e., they represent a composite of the mean values of measurable vocal characters obtained for all spectrograms that were studied. No diagnostic differences have been found between vocalizations of *ignota* recorded in Panama and in Ecuador, and the example shown in Fig. 1 and the data that follow represent combined values for recordings obtained in both countries. The only recording available from near the type locality of *ignota*, that of a loudsong, conforms closely to the example shown.

Visual examination of the spectrograms (Fig. 1) shows that the vocalizations of *ignota* are similar to those of *obscura* and differ from those of *brachyura*. Visually apparent in comparisons, the loudsong of *brachyura* is faster in pace (notes/sec) than those of *obscura* and *ignota*, and the central

notes of *brachyura* loudsongs are short and sharply downslurred sounding unmusical to the human ear, whereas those of *obscura* and *ignota* are longer and less steeply downslurred, having more of a musical quality. Less obvious visually, the pace of *brachyura* speeds up more than that of *obscura* and *ignota* (erroneously verbally described as the reverse in Isler et al. 1998 although the quantitative data were correct). In addition to the loudsong, *brachyura* and *obscura* deliver an abrupt note (Fig. 1B, G) that does not differ diagnosably between them (not yet recorded for *ignota*). However, a second type of call is clearly distinct. The second call of *brachyura* ($n = 4$) is a stereotyped trill (Fig. 1C), but those of *obscura* ($n = 12$) and *ignota* ($n = 4$) a downslurred note (Fig. 1E, H). The latter varies somewhat among individuals, as exemplified in Fig. 1, but is consistent in its essential characteristics.

Visual distinctions between loudsongs of *brachyura* (Fig. 1A) and those of *obscura* (Fig. 1D) and *ignota* (Fig. 1F) are supported by comparative analysis of measurements (data presented include the mean followed by the standard deviation and range). Comparing the entire loudsong, there was no overlap in ranges of the number of notes between *brachyura* loudsongs (28.3 ± 3.0 , 23–33 notes; $n = 11$) and loudsongs of *ignota* (17.4 ± 1.8 , 14–21; $n = 11$) and *obscura* (16.4 ± 3.2 , 11–22; $n = 19$) although only the difference between *brachyura* and *ignota* meets our test of significance. On the other hand, *brachyura* loudsongs are significantly faster in pace than loudsongs of both *ignota* and *obscura*; (11.3 ± 0.7 , 10.0–12.4 notes/sec) versus (6.6 ± 0.5 , 6.0–7.5) and (6.1 ± 0.6 , 5.0–7.0) respectively. Differences noted visually between the central notes of *brachyura* loudsongs and those of *ignota* and *obscura* are reflected in significant differences in the lengths of the middle notes; (28 ± 3 , 21–32 msec) versus (62 ± 5 , 54–71) and (62 ± 8 , 45–77) respectively. Finally, change in pace in the initial half of the song is reflected in the

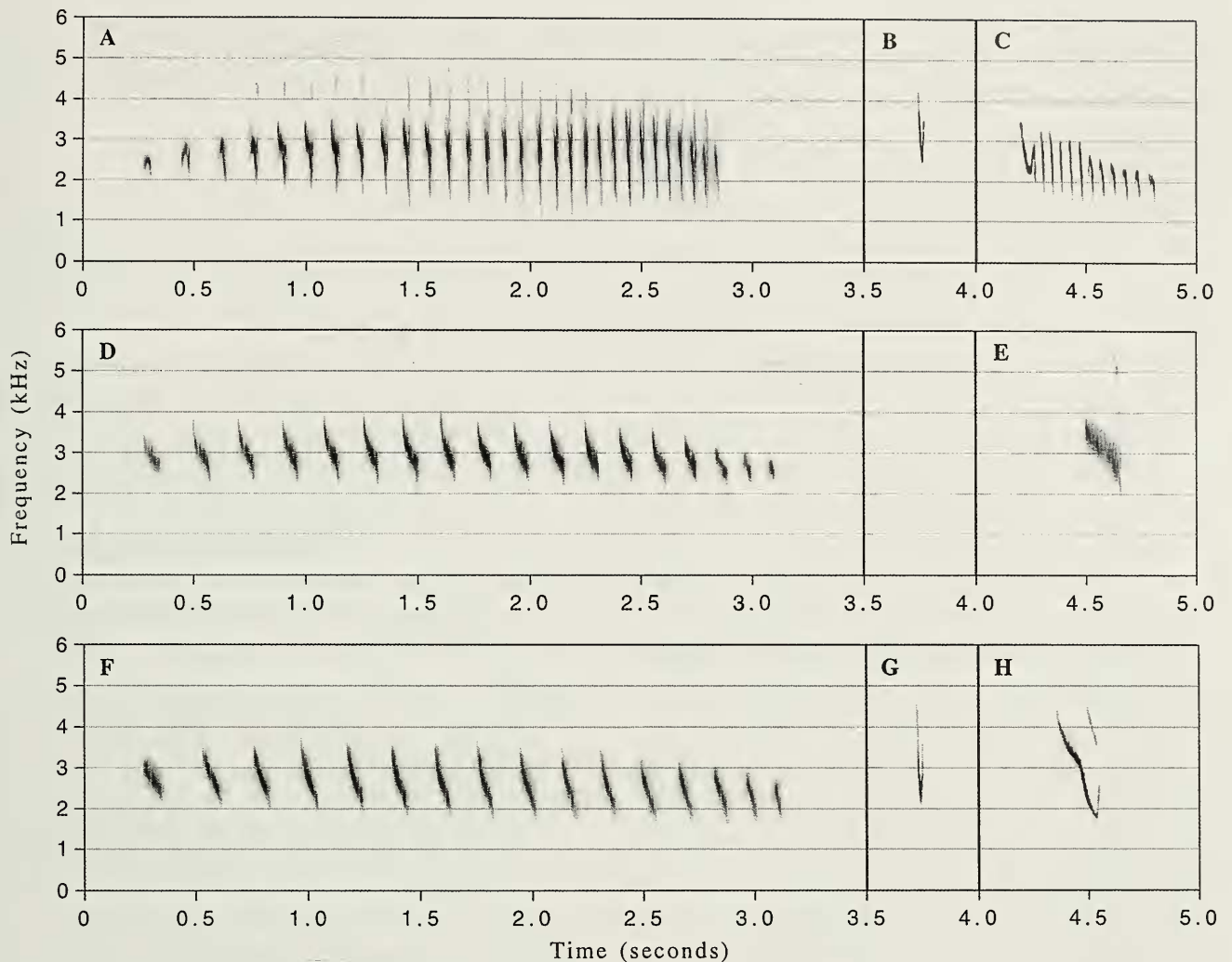


Fig. 1. Sound spectrograms of loudsongs and calls of taxa in the *Myrmotherula brachyura* complex. (A) loudsong of *brachyura* (Peru, Loreto, Quebrada Sucusari; ISL BMW.23:10; Whitney); (B) abrupt note of *brachyura* (Peru, Loreto, Quebrada Sucusari; ISL BMW.23:10; Whitney); (C) stereotyped trill of *brachyura* (Peru, Loreto, Quebrada Sucusari; ISL BMW.94:16; Whitney); (D) loudsong of *ignota* (Ecuador, Esmeraldas, 30 km SE of San Lorenzo; ISL DFL.5:01; Lane); (E) downslurred note of *ignota* (Ecuador, Esmeraldas, 30 km SE of San Lorenzo; ISL DFL.5:01; Lane); (F) loudsong of *obscura* (Peru, Loreto, Quebrada Sucusari; MLNS 30881; Parker); (G) abrupt note of *obscura* (Peru, Loreto, Quebrada Papaya; MLNS 29192; Parker); (H) downslurred note of *obscura* (Peru, Loreto, Quebrada Papaya; MLNS 29192; Parker). Identification data include location, archive number, and recordist. Acronyms for recording archives: MLNS = Macaulay Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca, New York; ISL = recordings not yet archived in an institutional collection but copied into an inventory maintained by the authors.

ratio between the duration of the second note and space and that of the middle note and space, with the higher ratios expressing a greater reduction in duration and hence a more rapid acceleration in pace; values of this ratio are greater for *brachyura* (1.73 ± 0.11 , 1.61–2.04) than for *ignota* (1.28 ± 0.10 , 1.08–1.44) and *obscura* (1.29 ± 0.08 , 1.18–1.47). In summary, four independent vocal characters differ diagnostically between *brachyura* and *ignota* and three between *brachyura* and *obscura*; vocal differ-

ences between *ignota* and *obscura* are insignificant.

Conclusions

Earlier studies have shown that *brachyura* and *obscura* are syntopic species that exhibit numerous diagnosable differences in vocalizations and morphology. Our comparison of *brachyura* and *ignota* demonstrates that these allopatric taxa differ to a similar extent vocally and morphologically

as do the sympatric *brachyura* and *obscura*. We therefore conclude that *brachyura* and *ignota* are specifically distinct, and we recommend that *ignota* be raised to species level. However, *ignota* and *obscura* cannot be separated vocally, and given the minimal morphological distinctions between them and recognizing the principle of priority, we recommend that *obscura* be considered a subspecies of *Myrmotherula ignota* under the Biological Species Concept (Johnson et al. 1999). Additional data and analysis, including genetic studies, are needed to confirm whether differences between *M. i. ignota* and *M. i. obscura* warrant their maintenance as subspecies, or conversely, that they deserve recognition as distinct species.

We propose the English name Moustached Antwren for *M. ignota*. The name reflects the wide black mystacial stripe characteristic of both subspecies. The name Short-billed Antwren, previously given *obscura*, is no longer appropriate because bill lengths of the newly constituted species overlap the bill lengths of *brachyura*. Nor do we believe that Griscom's Antwren, proposed for *ignota* if it were to be considered a distinct species (Ridgely & Tudor 1994), is satisfactory. In our opinion, Zimmer's detective work in discovering *obscura* is much more worthy of recognition than Griscom's minimal description of *ignota*, and it seems best to use a plumage feature as a basis for the English name.

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